Hybrid Forest Trees

by PALMER STOCKWELL and F. I. RIGHTER

Soon THERE will be hybrid forest trees that may grow to harvesting size in one-half or one-third the time required for a good, nonhybrid timber tree to reach the same size. Our forests and farm wood lots, where planting is practiced, might then be made to produce twice or three times the volume of timber that would be produced by planting standard stock or letting natural growth populate the site.

Already we have a hybrid pine, that at 3 years is more than twice as high and three times as heavy as the better of its two parents. So, a new era is beginning in reforestation and, although the hybridizing of forest trees seems to be at about the same stage that hybridization of corn had reached in the mid-1920's and failures and disappointments are to be expected along the way, we confidently predict that in another 20 years the forester will be using and discussing hybrid tree strains as casually as Midwest farmers now discuss their hybrid corn.

This exciting new development did not come overnight.

In the last decade, it has become increasingly apparent that the forests of the world are not producing timber as fast as the world needs it—particularly timber suitable for construction, packaging, paper making, and kindred uses. So, the tree breeder is at work in many countries, developing new strains to increase lumber production. Most countries are now interested in the improvement of forest trees, but intensive breeding work is carried on in relatively few of them.

Australia and New Zealand, which, like much of the Southern Hemisphere, lack softwood timber, have been leaders in introducing and acclimatizing foreign species. Not having the source materials needed for extensive hybridizing, Australian and New Zealand scientists have concentrated on selection and propagation.

The Russians have made contributions particularly with their research on hybrid oaks and poplars. The British are among the leaders in the development and analysis of ideas pertaining to the breeding of trees. The interest of Swedish breeders centered on the production of superior varieties of aspen for paper pulp production and conifers for construction lumber, the result being that several valuable new varieties are being used in forest planting. They have taken advantage of naturally occurring giant forms of aspen and have encouraged the introduction of hybrid poplars from America. Even during the war a few German research workers continued their quest for faster-growing trees. As in Sweden and Russia, the poplars have received most intensive attention in Germany, although the long-sustained German interest in the conifers continues. Denmark has made great strides in the work; indoor techniques for dwarfing trees, forcing early flowering, grafting imported scions on potted rootstocks, and other ingenious devices have reached a high stage of development.

The Union of South Africa established a tree-breeding program in 1943. Its first efforts are directed toward improving the native wattles and the introduced pines. South Americans are aware of the possibilities of tree breeding. Outstanding work has been done on quinine and rubber in the Amazon Valley of Brazil by commercial operators. Other Brazilian scientists are interested in various other species. In Argentina, Peru, Colombia, and other South American countries there is a growing interest, but they have established no specific tree-breeding program as yet. The Canadian tree-breeding program represents the combined action of the Biology Division of the National Research Council with the Dominion Forest Service and the Department of Agriculture of the Dominion. In 1940 the poplar work alone resulted in the production of 10,000 hybrids. The work was largely discontinued during the war but has gained impetus since then. The poplar for paper pulp and match stock production and conifers for paper pulp and construction lumber remain the centers of interest.

Between 1935 and 1945 most of the forest-tree breeding projects in the United States were reduced or discontinued, primarily because of the improved techniques for making paper of other woods than poplar, reduced budgets of Government-sponsored breeding work, and the war. The programs of the Oxford Paper Co. and the Tennessee Valley Authority were practically discontinued; those of the New York Botanical Garden, Harvard University, and the Northeastern Forest Experiment Station suffered almost as much. Only the Institute of Forest Genetics was able to continue its program—and its work was reduced by more than half during the war.

Several fundamental differences between the breeding of agricultural plants and forest trees should be kept in mind.

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In the breeding of agricultural plants, genetic uniformity is a necessity. For example, the varicolored corn of the Southwestern Indians cannot compete on the open market with uniform standard varieties. Lack of uniformity in a farm crop would spell financial ruin for the modern farmer. He enhances the natural uniformity of his crops still further by careful grading for size, color, and other qualities—a profitable practice.

But forest trees are genetically quite diverse, although they may appear to be uniform to the casual observer. Natural species owe their existence and perpetuation to variability, which enables some to survive attack by insects or disease and others to invade new environments or withstand changed conditions. Furthermore, the timberman is accustomed to using trees from forests of natural origin and variability does not disturb him as it would the farmer.

Breeding Forest Trees

To make certain of the uniformity and adaptability of new farm crops, long, carefully conducted field trials by the breeder are necessary. The average farmer cannot afford to risk the loss of his land and labor for a year to try out a new strain of unknown value. It may take as long as 20 years to produce and test a new form of an annual crop such as wheat before it can be safely recommended for use. In this respect the forester planter has a distinct advantage over the farmer.

By interplanting a hybrid or other new form with the standard strain or stock that would have been used throughout if the new form were not available, promising new trees may be put to use as soon as they are developed or discovered, without subjecting the forest owner to too much risk. The new trees can be planted at suitable intervals among a natural stand of young trees, or in every fifth row, or other selected interval, where an entire area is to be planted. Several advantages accrue. The new trees can be made to cover a greater acreage by interplanting, thus reducing the cost of using a new and relatively expensive form. If it proves to be superior, it will occupy the site at maturity, crowding out most of the slower-growing natural stand or standard strain.

A common practice is to plant 1,200 trees to the acre where from 100 to 200 trees are desired in the final stand of mature trees. This great excess of planting stock over expected mature trees represents another way in which forestry differs from agriculture. If, on the other hand, the new strain proves to be inferior to the natural stand or the planted standard strain, it will be suppressed and crowded out before the trees reach harvesting size. There would be no reduction of yield because the new form was a failure.

An objection, frequently voiced, to the use of hybrid trees is that, although the hybrids themselves may be superior to standard strain

trees, their offspring, the second generation hybrids, will be worthless, and in consequence the entire area would have to be replanted; whereas, if the standard strain were used, the area would be reseeded naturally from these trees and no subsequent replanting would be necessary.

This line of reasoning is applicable to some farm crop plants but it does not apply to forest trees. For example, *Pinus attenuradiata* is a hybrid between the Montercy and knobcone pines, produced at the Institute of Forest Genetics. The first generation hybrids, or F₁ plants, are reasonably uniform in growth rate and other characters. Seedlings from these trees representing the second generation of hybrids, or F₂ plants, show great variability. However, a considerable number of the trees (approaching 50 percent) are as good as the F₁ hybrid, and a few are even better. In a stand composed of this F₂ hybrid population there would be enough good trees of the second generation to repopulate the area and crowd out inferior trees before the stand reaches maturity. Another point is that although many hybrids of crop plants are sterile or practically so, pines are not; in fact, no sterile pine hybrid has yet been reported by anyone.

Besides an acceptable theoretical background for a hybridizing program, numerous techniques to assure the success of the program must be worked out. They will vary with the location of the breeding station, the kinds of trees used, and the individuals doing the work. Because it is impossible to cover all the new methods and techniques in use by tree breeders, a few typical examples based on experience at the Institute are selected.

Techniques that assure control of pollination are essential in plant-breeding work. Most of the genera of timber trees are wind-pollinated, and wind-borne pollen is usually a fine, dry, powdery dust that penetrates all but the most closely-woven fabrics. To find a material for pollination bags, many fabrics were sprinkled with pine pollen and examined under the microscope. A 10-ounce cotton duck was finally chosen because it is light, keeps out foreign pollen, and yet permits a slow circulation of air through the fabric, thus preventing condensation of water inside. The bags are fastened over the cone-bearing branch tips some time before pollen is shed from neighboring trees. The pollen to be used is collected before it starts to shed from the catkins. It is then extracted in the laboratory under conditions that prevent contamination by undesired pollen. At the time the cones are receptive, pollen is injected into the bags with a syringe.

Another serious problem arises when two species that are to be crossed flower or are ready for pollination at different times—sometimes several weeks apart. Usually, pollen is collected from the early form and used to pollinate the late form. At times, however, it is desirable to reverse the procedure, i. e., make the reciprocal cross. It has been necessary, there-

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fore, to work out methods for storing pollen from the late-flowering trees until the following year, when it can be applied to the early forms.

If pine trees are to be hybridized, the worker must have access to both pollen-bearing catkins and young seed-bearing cones. The poplars and certain other species will continue to develop flowers and mature the seeds when the branches are cut and placed in water; thus it is possible to carry out a hybridizing program indoors. That is not possible with the pines. It is necessary in pine breeding to climb the trees repeatedly. To avoid injuring the bark, a rope is thrown over the lowest branch and the geneticist climbs the rope. This strenuous but direct and effective method has been adopted because of the difficulty of transporting ladders or other heavy equipment on the forested mountainsides where the program of the Institute is carried out.

In experimental work time is of the essence, and research workers are always seeking short cuts. Increased growth rate being a most important objective of forest tree breeding, it is of major interest to learn as soon as possible the growth rate of a new hybrid. Recent work by John T. Buchholz of the University of Illinois gives promise that a pine hybrid of superior growth rate may be recognized by examination of some of the embryos even before the seeds mature. This would enable the breeder to evaluate the growth rate of a hybrid within 15 months, instead of waiting 3 to 5 years for the usual nursery trials to indicate its value before large-scale production is started.

At one time field trials of 10 to 20 years were deemed necessary to determine the growth rate of a tree. It is now known that seed size and time of germination affect the early growth rate of a tree but are not related to inherent vigor or ultimate size. In nursery tests, weighing the seeds and comparing trees from seeds of like weights eliminates the variation that would be introduced by using ungraded seeds. All seeds are stratified or packed in moist sand and moss at 40° F. for 60 days or longer. This treatment causes the seeds to germinate more or less simultaneously, eliminating effects due to difference in time of germination. If such factors are controlled, the growth rate of 2- to 3-year-old nursery-grown trees is a reliable guide to the inherent growth rate of the new form.

The Use of Hybrids

The use of hybrids offers exceptional opportunities for increasing crop production, and timber trees may here be considered simply as a forest crop. Tree strains that cross readily do not occur mixed together in the forest, else they would eventually "blend" into one form by hybridizing. We therefore find, except in a small number of specialized cases, that crossable species, varieties, or other categories of plants occupy different localities. Because hybrid trees are usually intermediate

between the parents in growth rate and other quantitative characters, the hybrid can be used to advantage in the region where the slower growing parent occurs.

A good example of this type of hybrid is that produced by using the pollen of a hybrid (Jeffrey pine × Coulter pine) on one of the parent forms (Jeffrey pine), the resultant hybrid being known as a backcross. Seeds of the backcross hybrid and of wind-pollinated Jeffrey pine were collected from the same parent tree and planted together in the seedbed. At 3 years of age the hybrid was 184 percent taller than the pure Jeffrey pine. Seeds from the pollen parent were not available, but pure Coulter pine seedlings grow at about the same rate as the backcross hybrid. The hybrid, therefore, will be planted in the range of the slower growing parent, the Jeffrey pine.

Another intermediate type of hybrid is that obtained by crossing the poorly formed, and not very desirable jack pine of the Lake States with the straight-growing lodgepole pine of the Sierra Nevada. At 3 years of age the hybrid trees approximate or slightly exceed the height of pure jack pines and are 179 percent of the height of lodgepole pine. The logical locality in which to use this hybrid in forest planting is where jack pine is now planted, because the hybrid has the straight, erect growth habit of the lodgepole pine.

While the intermediate type of hybrid has a definite field of usefulness, there is another type of hybrid with even greater potential value. This is the type that shows hybrid vigor or, to the geneticist, heterosis. This phenomenon, although not yet fully understood, is of tremendous value to the agricultural world. It is hybrid vigor that makes some of the poplar and pine hybrids grow at twice or more the rate of the parental forms. This means that a timber tree adaptable to the location and having hybrid vigor may grow to harvesting size in one-half or one-third the time required for a good, nonhybrid forest tree to reach the same size.

The hybrid between the eastern and the western white pines, as an example, shows greater growth capacity than either parent. At Placerville the two parent forms grow at approximately the same rate, but the average hybrid at 3 years of age was 232 percent of the height of the seed parent, the western white pine. The difference in volume, or weight, was even greater. At 4½ years the cut-off top of the largest eastern white pine seedling weighed 64 grams, that of the largest western white pine 72 grams, and that of a large (but not the largest) hybrid seedling 232 grams, or 322 percent of the weight of the better parent. This hybrid warrants trial wherever white pines are planted for timber production. It is being tested for resistance to blister rust by Dr. Willis Wagner, of the Department of Agriculture.

With hybrid trees, as with other new things, costs and quantity production must be considered. A record has been made of the cost, in

man-days, of hybrid seeds and of the quantity of seeds it is possible to produce. In pine hybridizing, bags are placed over the young conelets that are to be pollinated. This precaution prevents contamination by air-borne pollen of the forest. Because this technique is always used, the bag is a convenient unit of measurement of effort. What is termed a 1,000-bag program carried out by skilled and experienced workers on large trees in the forest would require from 30 to 45 man-days. (The requirements and yields of the 1,000-bag program are estimates based on the use of only a few dozen bags, as manpower shortage has prevented carrying out a 1,000-bag program for any single cross.) The yield per 1,000 bags has varied from 6,500 hybrid seeds for the poorest to a maximum of 432,000 hybrid seeds for the best yield.

By applying the interplanting method, that is, using hybrid seeds for every sixth row, for example, at a spacing of 6 feet by 6 feet, and deducting 40 percent from total seed number for possible losses, the acreage that could be planted per 1,000-bag breeding program would range from a minimum of 19.5 acres to a maximum of 1,296 acres. As more experience is gained, costs no doubt can be reduced.

In some genera of trees hybrid vigor is rare. In others, such as the poplars and the pincs, hybrid vigor is more frequent. To date, there is no predicting which crosses will exhibit hybrid vigor and which will not. Of the 12 hybrids between pine species produced at the Institute since 1940, 4 show definite hybrid vigor at 3 years and 1 or 2 others, as yet too young to evaluate, look promising. The remainder are intermediate. Trees that show hybrid vigor will probably become the most used planting stock of the future. Standard strains or intermediate hybrids will have little appeal for the forest planter, except in special cases where resistance to insects, disease, or drought may influence the decision.

Thus far, few hybrid trees have been used in forest planting. R. H. Richens of Great Britain, in the most complete review to date of the literature of tree breeding, lists 405 forest-tree hybrids. Of these, only 54 are coniferous trees, which yield the greater part of the world's construction lumber, while 351 are hybrids of nonconiferous species that are used for paper pulp, cabinet work, match stock, et cetera. The world, facing a rapidly shrinking supply of timber, is looking for some means of relieving the situation. There is a rapidly increasing pressure to try out hybrid trees in forest planting. The indication that fast-growing hybrids can be produced in abundance, together with the possibility that financial risk can be reduced during the necessary trial period by interplanting the hybrids with known varieties, tends to increase interest.

This trend is international in scope. There is hardly a week that does not bring inquiries from foreign lands to the Institute of Forest Genetics. Some of these inquirers wish to send young men for training in hybrid-

seed production. Others want information on methods of hybrid production and still others wish to have hybrid seed sent to them.

As for plans in this country—there will be a large increase by many agencies in hybrid planting, both of the hardwoods, such as poplar and chestnut, and the coniferous species, such as the pines. As many hybrids are being produced at the Institute of Forest Genetics as the available manpower permits. Two or three of the most promising new hybrids are being used in this effort. The California Region of the United States Forest Service has started to use the hybrids in forest plantings throughout the State, giving them an actual field test under a wide variety of conditions.

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FOR FURTHER READING

- Buchholz, John T.: Embryological Aspects of Hybrid Vigor in Pines, Science, volume 102, No. 2641, pages 135-142, 1945.
- Mackenzic, C. J.: Twenty-eighth Annual Report of National Research Council of Canada, page 15, 1944-45.
- Ness, H.: Possibilities of Hybrid Oaks, etc., Journal of Heredity, volume 18, pages 381-386, 1927.
- Richens, R. H.: Forest Tree Breeding and Genetics, Imperial Agricultural Burcaux Joint Publication, No. 8, 1945.
- Righter, F. I.: New Perspectives in Forest Tree Breeding, Science, volume 104, No. 2688, pages 1-3, 1946.
- Stockwell, Palmer, and Righter, F. I.: Pinus: The Fertile Species Hybrid Between Knobcone and Monterey Pines, Madrono, volume 8, No. 5, pages 157-160, 1946.
- Syrach, Larsen C.: De enkelte arters anvendelse, Proveniens og foraedling, Svenska Skogavardsforeningens Tidskrift, volume 41, pages 182-199, 1943. (Plant Breeding Abstracts, volume 14, page 999, 1943.)
- Wettstein, W. von.: Possibilities of Breeding New Ecotypes after Hybridization, Der Zuchter; Zeitschrift fur Theoretische and Angewandte Genetik, volume 14, pages 282-285, 1942.